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Research

Soil fauna diversity and chemical stressors: a review of knowledge gaps and roadmap for future research

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Soils harbour highly-diverse invertebrate communities that play important roles for ecosystem services, including the mitigation of environmental pollution. Chemical stressors, such as pesticides, pharmaceuticals and metals, are being increasingly spread into ecosystems due to human activities. While it is crucial to predict the consequences of chemical stressors for soil biodiversity, chemical toxicity is often assessed using individuals or populations in laboratory cultures. There has been no systematic evaluation of the evidence documenting the impacts of chemical stressors on diverse, natural soil communities. Here, we use a comprehensive literature review of 274 studies to evaluate the current state of knowledge about the effects of chemicals on soil fauna communities. Most research has had limited spatial scope, with noteworthy gaps in the regions that are potentially the most threatened by soil pollution (Southern Hemisphere). Furthermore, reports generally were constrained to a few emblematic soil fauna groups (nematodes, collembola and earthworms) and chemical stressors (metals). Future research should address biases in spatial distribution of studies, as well as the taxonomic groups and chemical compounds considered. Specifically, emphasis on indirect effects mediated by species interactions, ecosystem functioning and interactive effects of stressors and climate change, currently lacking in the literature, is needed to improve soil-biodiversity conservation and restoration efforts, as well as predictions of global diversity change.

Keywords: biodiversity, ecosystem functioning, multiple stressors, pollution, soil fauna, systematic review

Introduction

Soils host one quarter of all species on Earth, and these species play crucial roles in many ecosystem functions and services (Bardgett and van der Putten 2014). Soil fauna are incredibly diverse with organisms spanning a wide range of sizes (μm to m), shapes and functional roles (e.g. decomposers, plant-parasites, predators) (Decaëns 2010, Bardgett and van der Putten 2014). However, soil biodiversity is facing multiple



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threats related to human activities (Blankinship et al. 2011, Veresoglou et al. 2015, Geisen et al. 2019b). Among those threats, some (e.g. climate change) are far more studied than others (e.g. pollution), leading to a potentially biased view of human impacts on soil biodiversity (Bernhardt et al. 2017, Mazor et al. 2018).

Chemical stressors, such as pesticides, pharmaceuticals or metals, are being increasingly released into the environment due to various human activities (agriculture, industry, waste management, etc.) (Wang et al. 2020). Soil pollution by chemicals has been identified as one of the main threats to soil functioning worldwide (FAO 2018). In fact, the rates of change in the production of chemical stressors can surpass those of other global change drivers, such as climate change (Bernhardt et al. 2017). Despite these trends, the field of ecology has paid less attention to chemical pollution compared to other drivers of global change (Bernhardt et al. 2017, Mazor et al. 2018), reflecting a traditional divide between ecological and ecotoxicological research (Clements and Rohr 2009, Gessner and Tlili 2016). Therefore, chemical stressors represent an important but under-recognized global change driver (Fig. 1).

The impacts of chemical stressors on biodiversity have been mostly investigated at the level of individual organisms or populations, giving limited insights into the more complex, and thus more realistic, responses of soil communities, food webs and ecosystem processes (Beketov

and Liess 2012, De Laender and Janssen 2013, Gessner and Tlili 2016). However, the impacts of chemical stressors can extend to the continent-level (Malaj et al. 2014), effectively impairing multiple aspects of biodiversity and ecosystem functioning through cascading effects within food webs (Yamamuro et al. 2019). Indeed, the ecological consequences of chemical pollution for ecosystems not only depend on direct toxic effects on organisms that are often the focal point of ecotoxicological studies, but also on indirect effects mediated by species interactions (Rohr et al. 2006, Yamamuro et al. 2019). Furthermore, environmental conditions determine the response of communities to chemical stressors, and, therefore, assessing the interactions with other global change drivers is a crucial further step (Rillig et al. 2019, Bowler et al. 2020). Following numerous calls for incorporating ecological theory into ecotoxicology (Van Straalen 2003, Clements and Newman 2006, Relyea and Hoverman 2006, Clements and Rohr 2009, Beketov and Liess 2012, De Laender and Janssen 2013), recent efforts have focussed on the indirect effects of chemical stressors, the consequences for ecosystem processes, as well as the interactive effects of stressors and other factors of global change in aquatic realms. Such research has been compiled for aquatic ecosystems (Relyea and Hoverman 2006, Gessner and Tlili 2016). No similar overview exists for describing terrestrial research approaches and how well they capture the ecological consequences of soil pollution

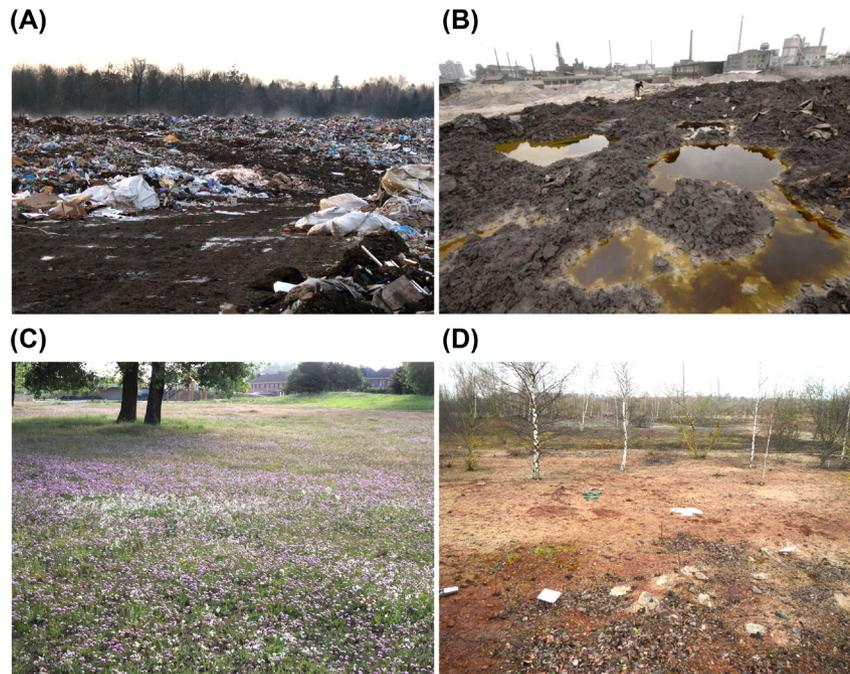


Figure 1. Soil pollution and contamination are important but under-recognized global change drivers in ecology. Soils can be visibly affected by human and industrial activities (A): dumping site in Ukraine, (B): industrial soil pollution in China), but pollution and contamination are often invisible (e.g. in France), (C): site historically polluted with metals but hosting highly specific, metal-tolerant, plant species and (D): former settling pond of iron industry with a diversified vegetation developing on a soil containing metal-rich sludge). Photo credits: (A) Andy Shustykevych, Creative Commons Attribution-Share Alike 3.0 Unported license; (B) JungleNews, Creative Commons Attribution Share Alike 4.0 International License; (C) Guillaume Lemoine; (D) Apolline Auclerc.

across the wide range of taxonomic groups living in soils (Orgiazzi et al. 2016) and of different types of pollutants (FAO 2018). What are the main knowledge gaps and how do they influence our understanding of ecosystems? What are future research directions that would address such knowledge gaps?

Here we present the most comprehensive review to date of the field of soil pollution impacts on soil fauna. We review 274 published articles reporting the impacts of a wide range of chemical stressors on soil fauna communities across the planet. Given the disparate nature of these studies, we adopted a vote-counting approach, rather than a quantitative meta-analysis. We identify the current knowledge gaps regarding soil community and ecosystem responses to stressors that restrict a general understanding of the ecological consequences of exposure to chemicals in soil. Based on the present assessment of the existing literature, we present critical recommendations for future research avenues and experiments, which are especially relevant to scale up the response of soil communities to consequences for soil ecosystem functions and ultimately ecosystem services.

Methods

Searching the literature

We conducted a systematic literature search as part of a global meta-analysis focussing on the impacts of various global change drivers on soil fauna (Phillips et al. 2019a) on 15 October 2018. The literature search strategy is fully reported in Phillips et al. (2019a). This global meta-analysis addresses a wide breadth of global change drivers, including but not limited to chemical pollution, with the aim to compare the effects of different types of global change drivers on soil fauna. There were three main inclusion criteria for the global meta-analysis. First, the study had to report the response of soil fauna to one or many global change drivers (chemical stressors, climate change, nutrient enrichment, land-use intensification, land-use change, habitat fragmentation or loss, and invasive species) in terms of abundance, biomass or diversity. Second, the study had to focus on natural soil communities (laboratory experiments were included if they exposed non-sterilized, intact soil cores containing organisms, but were excluded if they created artificial communities by adding different species to soil microcosms). Third, the sampling procedure had to involve soil and/or litter processing methods. Studies involving only pitfall trap sampling were not included as they collect a large number of organisms that only dwell on the soil surface. This approach allowed us to focus on organisms strictly living below-ground. It is important to note that this approach, may limit the breadth of studies focusing on some soil taxa, such as gastropods, spiders, ants and termites that are often sampled by the means of pitfall traps. Nevertheless, these taxa are also sampled by the means of soil and/or litter processing methods, and are thus represented in our set of studies.

From that systematic search (Phillips et al. 2019a), we identified 274 studies that looked at the influence of a wide range of chemical stressors for the present review (Supporting information). We focussed on the studies reporting soil fauna diversity and abundance at sites affected by pollution or contamination (observational studies), or in experimental treatments involving chemical stressors additions. A wide range of chemical stressors were considered according to a recent FAO report on soil pollution (FAO 2018): metals, pesticides, persistent organic pollutants, PCBs (polychlorinated biphenyl), PAHs (polycyclic aromatic hydrocarbons), pharmaceuticals, plasticizers, nanoparticles, radionuclides or radiation. Although ionizing radiations are not chemical stressors per se, they are emitted by radioactive substances and we included them into the broad term ‘chemical stressors’ in the present review, in line with the FAO report (FAO 2018). Studies looking at nutrient enrichment or deposition were not included. Studies had to report observed or applied pollutant concentrations at the studied sites (e.g. concentrations in the soil, pesticide application rates) either in the paper itself, or in a previously-published study.

Although our search strategy was not limited to papers published after 1990, the final included papers were mostly published after 1995. This result may be due to the database (Web of Science) and strict inclusion criteria that we used to compile the list of studies. Indeed, older papers tended to lack a DOI, their full texts were more difficult to retrieve, and they were often not meeting our criteria regarding contaminant quantifications as well as means and standard deviations for soil fauna data. It is unlikely that our conclusions regarding knowledge gaps and future research directions would change by adding older publications. However, future quantitative syntheses would benefit from a broader literature search including older publications as well as grey literature and non-English publications (Koricheva et al. 2013, Konno et al. 2020).

Mapping the gaps

To identify the main knowledge gaps in the research field, we collected meta-data of the 274 relevant papers by screening the full texts for the following information:

- Country where the study was conducted, in order to create a map of pollution research and identify areas less well covered.
- Soil fauna groups assessed using the global soil biodiversity atlas classification (Orgiazzi et al. 2016), with the aim to identify the most and least studied groups.
- Main pollutant types (using the classification by Rodríguez-Eugenio in FAO 2018), in order to identify the most and least studied chemical stressors.
- Human activities causing the pollution (FAO 2018): industrial, agricultural/livestock, mining/smelting, waste/sewage, natural/geogenic origin (for metals), or other sources (such as accidental spills, or experimental addition of a pollutant to simulate a disturbance or to suppress soil fauna in order to investigate their functional role).

Addressing the ecological perspective

One of our aims was to investigate the scope of studies that tested stressors' impacts on soil fauna. To that end, we recorded information related to three main topics: biodiversity and food webs; ecosystem functioning, and interactive effects between stressors and other global change drivers (Clements and Newman 2006, Beketov and Liess 2012, De Laender and Janssen 2013, Gessner and Tlili 2016).

Biodiversity and food webs. We recorded whether the study reported soil fauna responses in terms of abundance, biomass, taxa richness or other metrics of biodiversity (Shannon's index, evenness). We assumed that studies looking not only at the response of soil fauna, but also that of other ecological groups (above-ground invertebrates, plants, microbes, etc.) would be more likely to incorporate a multi-trophic context and to address the indirect effects of stressors on soil fauna, as mediated by species interactions. We therefore recorded if the study reported the response of other ecological groups and which groups were investigated (e.g. plants, micro-organisms, above-ground arthropods, birds, amphibians, etc.).

Ecosystem functioning. We recorded if the study measured one, several or no ecosystem functions. Defining what is an ecosystem function is subjective (Manning et al. 2018). Here, we followed the authors' statements in their papers to decide whether any given study measured an ecosystem function. Papers had to specifically state that they were measuring ecosystem functioning (we searched for combinations of the terms 'ecosystem', 'function', 'process' in the main texts). In addition, we recorded 13 papers that measured decomposition (leaf litter mass loss or respiration) or plant productivity (crop yield or any component of plant biomass), without mentioning the terms ecosystem function or process. We decided to deliberately include these papers although they formally did not mention the key terms because they clearly studied ecosystem functions (Gessner et al. 2010, Tilman et al. 2012), and formed a large part of the studies involving ecosystem functions that would otherwise have been ignored.

Multiple drivers of global change. We further recorded whether the study focussed only on chemical stressors, or also investigated combined effects of stressors with other drivers of global change (climate change, nutrient enrichment, habitat fragmentation or loss, invasive species, land-use intensification and land-use change). Multiple-driver studies included studies with full factorial designs (where each driver was studied separately and in all possible combinations). Multiple-driver studies also included study designs where the different drivers were studied separately but not in combination, as well as designs addressing only the combined effect of different drivers (separate effects of different drivers cannot be disentangled in this case). We reviewed those papers and counted how many incorporated full-factorial designs enabling investigations of the interactive effects of multiple drivers.

The R software was used to create the figures using the R packages 'ggplot2', 'ggmap', 'viridis', 'alluvial' and 'patchwork' (Bojanowski and Edwards 2016, Garnier et al. 2018,

<www.r-project.org>, Kahle et al. 2019, Wickham et al. 2020, Pedersen 2020).

Mapping knowledge gaps in soil pollution impacts on fauna research

We found 274 studies focussing on chemical stressors' impacts on soil fauna communities (the full list of references is reported in the Supporting information). We first investigated knowledge gaps in terms of geographic location, taxonomic groups and pollutant types in order to highlight potential avenues for future research aiming to close those gaps (Fig. 2).

Geographical bias. Is soil pollution research biased towards areas that are potentially less polluted?

Studies covered the entire globe, but were mainly located in the Northern Hemisphere (Fig. 2A). With more than 20 studies per country, France, USA and China were the most represented. In line with many global-scale syntheses of biodiversity (Delgado-Baquerizo et al. 2018, Phillips et al. 2019b, van den Hoogen et al. 2019, Guerra et al. 2020), this result may reflect research funding inequalities between countries in the Global North and South (Maestre and Eisenhauer 2019). This is particularly concerning as many countries of the Global South are threatened acutely by soil pollution (FAO 2018). While countries of the Global North are also affected by soil pollution (FAO 2018), several policies and infrastructures, such as the water framework directive in the EU, regulate chemical stressors, with documented benefits for biodiversity (van Klink et al. 2020).

There are only a few global initiatives and maps showing the distribution of pollutants across the planet and across different types of pollutants (Shen et al. 2013, Sonter et al. 2018, Maggi et al. 2019, FAOSTAT 2020). Based on these estimates, there is a clear mismatch between the areas potentially the most polluted and where the studies addressing chemical stressors' impacts on soil fauna communities have been conducted (Fig. 2A).

These results highlight the geographical areas where future research should be targeted in order to give a better global coverage of soil fauna responses to pollution. Overall, low- and middle-income countries from the Global South should be prioritized, which is in line with FAO (2018). Since the sensitivity of organisms to chemicals depends on both the species, and on abiotic parameters such as temperature and water availability (Holmstrup et al. 2010), there could be different responses in warmer and drier climates compared to temperate areas (Chapman et al. 2006, Kwok et al. 2007). Understanding if the responses of soil communities differ between biomes across the globe is therefore an important future research area.

Pollutant type bias. Evolution of interest in different pollutants through time

Studies spanned from 1991 to 2018, and addressed the effects of a wide range of chemicals (Fig. 2B). We find continued

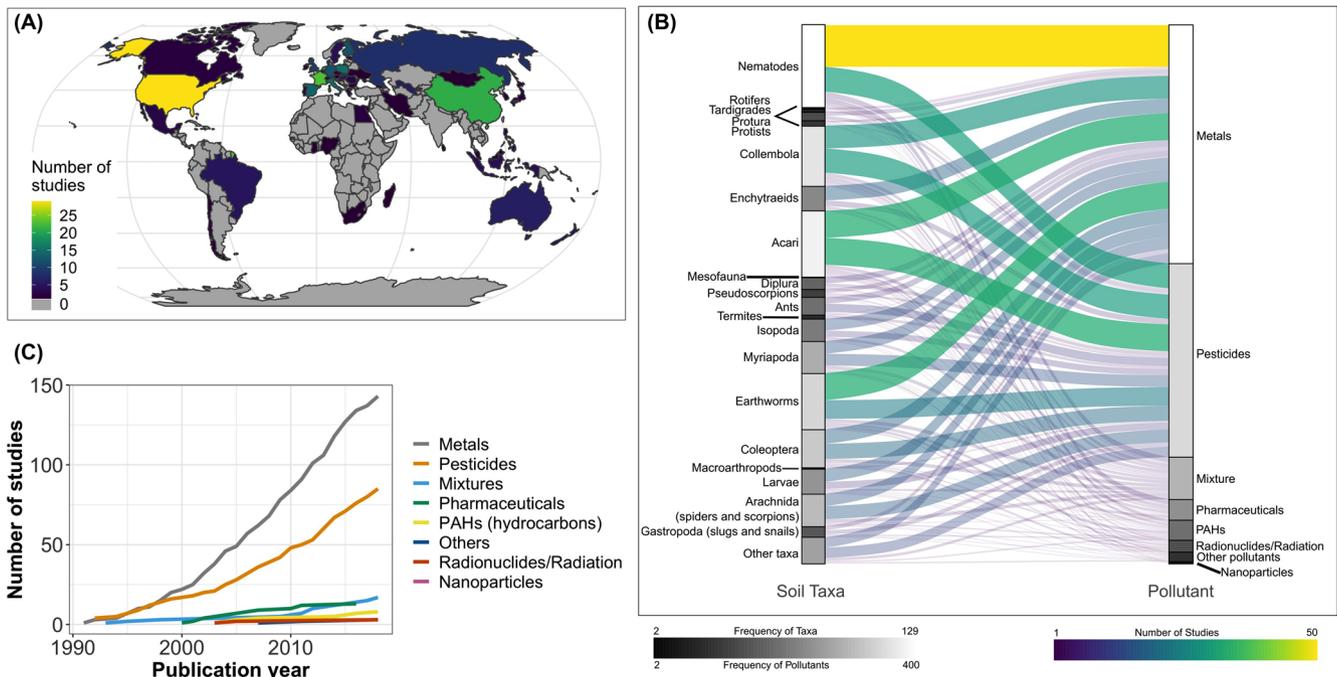


Figure 2. Mapping knowledge gaps regarding chemical stressors' effects on soil fauna. (A) Geographical coverage, by country where the studies were conducted, of the 274 studies, showing limited knowledge in the Global South. (B) Cumulative number of studies on each type of pollutant studied through time (mixtures: papers addressing several categories of pollutants). (C) Alluvial diagram showing that a few emblematic taxonomic groups and pollutant types dominate research. The size of each box is proportional to the number of studies per taxonomic group (left) and pollutant (right). Link width (and colour) is proportionate with the number of studies containing both topics. Taxonomic groups are sorted by increasing body size category (microfauna, mesofauna and macrofauna groups), and within body size categories by decreasing frequency in the dataset. Pollutants are sorted by decreasing frequency.

interest in metals and pesticides impacts on soil fauna across the time span of the studies, with a high number of papers for these two categories of chemicals (Fig. 2B). Industrial and mining activities and agricultural practices are and have been main human sources of widespread soil pollution, especially since the Industrial and Green Revolution of the 19th and 20th centuries (Nriagu 1996, Bommarco et al. 2013, FAO 2018). While pesticides are applied on large spatial scales (Humann-Guillemot et al. 2019), mining activities generally have more localised impacts (Sontner et al. 2018). However, industrial activities such as smelting can lead to atmospheric deposition of metals contaminating large areas (Fritsch et al. 2010). The wide spatial and temporal extents of pollutions with metals and pesticides can therefore explain the continuous interest in their effects on soil communities highlighted here (Fig. 2B).

Fewer studies addressed PAHs ($n = 19$ studies) and emerging pollutants such as pharmaceuticals ($n = 14$), nanoparticles ($n = 2$) and plastics and plasticizers ($n = 2$). The number of these studies has grown more slowly and only started increasing in recent years (Fig. 2B). These results can be explained by recent technological advances enabling to measure low concentrations of a wide range of chemicals in soil samples (Adriano 2001). Furthermore, pollution caused by urban and transport infrastructures that are associated with PAHs and metal inputs to soils were less studied (18 studies, versus 104 and 100 studies for industrial and agricultural activities respectively). Given the

rapid expansion of urbanized areas (McDonald et al. 2020), future research is needed to address how soil communities are affected by pollution associated with urban areas.

A few studies addressed multiple types of pollutants, and this number increased over time ('Mixtures', Fig. 2B). This pattern likely reflects the increasing interest in more realistic scenarios, where multiple types of pollutants are simultaneously affecting soil ecosystems (Schaeffer et al. 2016, Silva et al. 2019). It must be noted that here, the number of studies in the mixture category is only capturing studies addressing multiple chemicals across different categories, but not within categories (e.g. multiple metals or multiple pesticides). Mixtures of chemicals are an issue almost everywhere, and although people have started studying them early on (Fig. 2B), the number of papers studying mixtures has only very slightly grown. Given the ubiquity of co-occurring chemical stressors affecting ecosystems (Backhaus and Faust 2012, Cedergreen 2014, Schreiner et al. 2016, Silva et al. 2019), future studies need to address this important knowledge gap, both within and across categories of chemical stressors.

Taxonomic bias. Soil pollution research is clustered towards a few groups of organisms

The most represented soil fauna groups were nematodes ($n = 119$), mites (Acari) ($n = 95$), springtails (Collembola) ($n = 87$) and earthworms ($n = 81$) (Fig. 2B). These groups are

emblematic and well-known soil organisms that have a strong influence on many ecosystem processes (Darwin 1881, Rusek 1998, Coleman et al. 2004, Ferris 2010, Orgiazzi et al. 2016), therefore their predominance in these studies is not surprising. In addition, nematodes, mites, Collembola and earthworms are often used as bioindicators of soil quality (Römbke and Breure 2005, Fründ et al. 2010), although other soil taxa are relevant bioindicators as well (Jänsch et al. 2005). Many case studies included in the present review used the abundance and diversity of these bioindicator groups to quantify the extent to which soil contamination was associated with ecological impacts and poor soil health (Paoletti et al. 1998, Santorufo et al. 2012, Wahl et al. 2012).

These results highlight opportunities for global synthesis approaches focussing on nematodes, mites, Collembola and earthworms (Fig. 2B). The global distribution maps available for these groups (Phillips et al. 2019b, van den Hoogen et al. 2019, Potapov et al. 2020), could be combined with global maps of soil pollution to assess patterns across pollutant types and soil fauna groups. Such an approach will enable to reach more generalizable predictions of the impacts of chemical stressors on soil fauna communities across environmental conditions. They will further enable scientists to test if environmental quality criteria, derived from laboratory experiments, also protect soil fauna in naturally diverse communities. Finally, even for emblematic soil fauna groups, we observed limited knowledge related to their response to emerging pollutants (Fig. 2B), highlighting the need for more studies on this topic.

Our review further reveals important knowledge gaps for neglected groups of soil organisms. This is especially the case for soil micro- and mesofauna, where rotifers ($n=2$), tardigrades ($n=4$), protists ($n=7$), pseudoscorpions ($n=12$), Protura ($n=13$) and Diplura ($n=17$) were poorly represented compared to nematodes, earthworms, mites and Collembola (Fig. 2B). Overall, 106 studies reported the response of taxonomic groups belonging to macrofauna (such as Coleoptera ($n=55$), Arachnida (spiders and scorpions) ($n=47$), Myriapoda ($n=46$), Insect larvae ($n=36$), Isopoda ($n=32$)). The number of studies per taxonomic group belonging to macrofauna was slightly more balanced than for groups belonging to micro- and mesofauna (Fig. 2C). This is probably because macrofauna studies usually covered many different taxonomic groups, while micro- and mesofauna studies often focussed on target taxonomic groups (e.g. nematodes or Collembola). This pattern may also reflect our literature search, that used broad search terms to encompass the diversity of soil macrofauna (such as soil (macro) fauna, arthropods or invertebrates). There were few studies reporting the response of ants ($n=26$), gastropods ($n=16$) and termites ($n=5$) despite the functional importance of those three groups. This is probably due to our inclusion criteria for sampling methodology, which excluded pitfall trap data. The geographic bias towards temperate regions probably further explains the limited data on termites. We decided to exclude studies using pitfall traps, as data derived from this method

represents activity densities rather than abundances/diversity in a certain area.

The taxonomic gaps highlighted here likely reflect the lack of taxonomic expertise for those groups of soil fauna. This result could also reveal a publication bias toward sensitive taxa used as bioindicator species. For example, tardigrades could be underrepresented because they are resistant to many disturbances, such as drought and freezing (Guidetti et al. 2011). Future synthesis approaches of stressors' impacts across soil fauna groups will reach biased estimates if such a publication bias is not addressed and overcome (Koricheva et al. 2013). By mapping taxonomic knowledge gaps in soil pollution, we highlight opportunities for future soil biodiversity research to focus on these neglected groups. This is important, not only for modelling global diversity scenarios, but also because these groups could play important roles in ecosystem functions (Coleman and Wall 2015). Moreover, different groups of soil organisms were shown to differ in their global biodiversity distribution, indicating variations in their main drivers (Bastida et al. 2020). A first step will be to gain more basic knowledge about the biology and ecology of those different groups as they are overall poorly studied (Orgiazzi et al. 2016). This will be crucial to understand how they may respond to global change drivers, including chemical stressors.

Overall, our review reveals that addressing neglected regions of the world, emerging chemicals (such as pharmaceuticals, plastics), multiple combined stressors and neglected taxonomic groups are main future directions that would improve our understanding of chemical stressors' impacts on soil fauna communities. Beyond these general recommendations, our results identify the specific scenarios that deserve future attention or for which sufficient information is already available to conduct quantitative synthesis work (Fig. 2). The next step will be to relate the impacts of chemical stressors on soil fauna with their consequences for ecosystem processes.

Taking an ecosystem perspective

We analysed the scope of research on chemical stressors' impacts on soil fauna by focussing on three main topics: multi-trophic biodiversity, ecosystem functioning and multiple drivers of global change (Fig. 3) (Relyea and Hoverman 2006, Clements and Rohr 2009, Beketov and Liess 2012, De Laender and Janssen 2013, Gessner and Tlili 2016).

Multitrophic biodiversity responses and food webs

Our review highlights the limited knowledge on the response of soil food webs to chemical stressors, which is an important gap given the dependence of ecosystem functioning on species interactions in the underlying food webs (Hines et al. 2015, Barnes et al. 2018, Wang and Brose 2018). Across the studies, the number of soil fauna taxonomic groups considered varied from 1 to 14. Most studies reported the response of a single taxonomic group of soil fauna ($n=161$), and

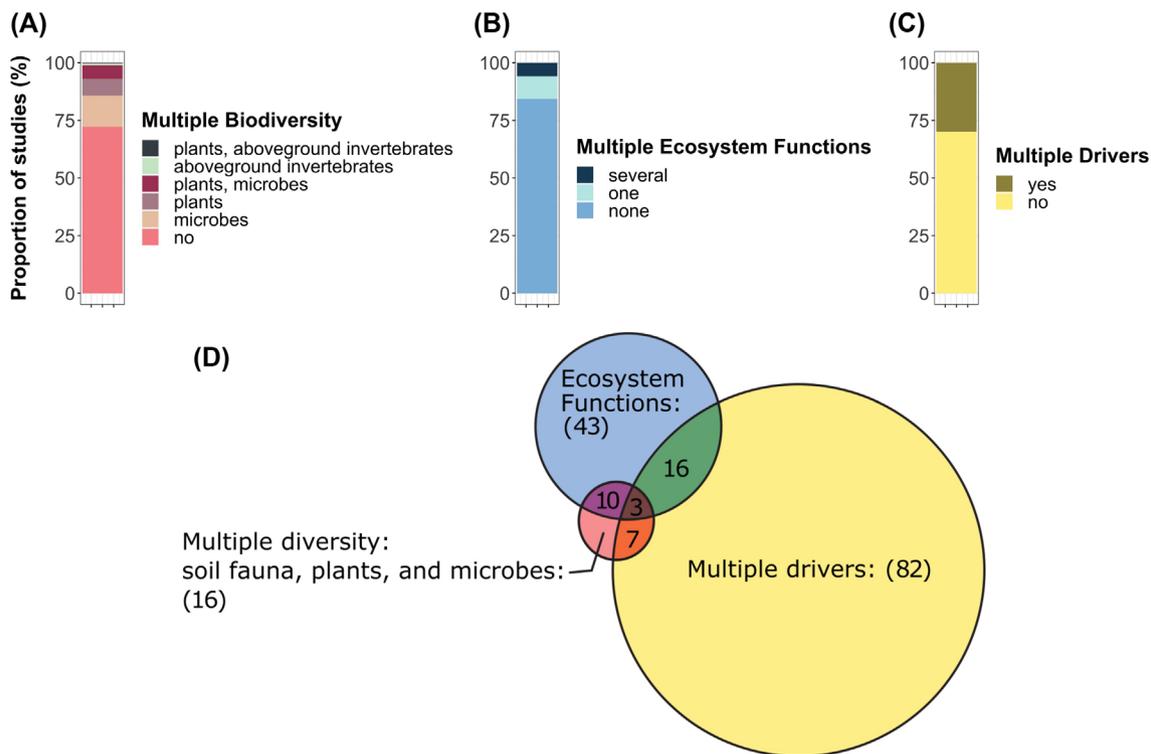


Figure 3. Ecosystem perspective of soil pollution research. Studies addressing multiple ecological groups in addition to soil fauna (A), ecosystem functioning (B) and response to combined chemical stressors and other drivers of global change (C, climate, land-use intensification, land-use change, habitat fragmentation and loss, invasive species or nutrient enrichment). (D) shows how studies jointly covered those three topics (Venn diagram with the area of each circle proportional to the number of studies that did include multiple diversity, ecosystem function and/or multiple drivers).

only 65 studies reported more than three taxonomic groups. Furthermore, few studies investigated biodiversity, not only of soil fauna, but also of other ecological groups either below or aboveground ($n=76$, Fig. 3A). Such multi-trophic and multi-diversity studies are needed to reveal the cascading consequences of chemical stressors (Rohr et al. 2006, Clements and Rohr 2009). For example, it is well known that changes in a species dominance will influence other species through species interactions, consequently altering community structure and dynamics (Wootton 1994, Schmitz et al. 2000, Scherber et al. 2010). Studying the indirect effects of chemical stressors on biotic interactions, both within and between trophic levels, is particularly important to predict the long-term consequences of chemical stressors for soil fauna. In addition, such approaches are necessary to predict how soil fauna mediate stressors' impacts on other important functional groups (such as plants), or on rare and endangered species (such as birds, or amphibians, for which soil fauna is an important food source).

Here, studies that addressed the response of multiple ecological groups to chemical stressors mostly considered soil microbes or plants in addition to soil fauna ($n=37$ and 20, for microbes and plants (including lichens), respectively, Fig. 3A). The responses of the three ecological groups together (i.e. microbes, plants and soil fauna) were addressed in 16 studies (Fig. 3A, Supporting information). In soils,

microbes, plants and fauna are highly connected, and their interactions are crucial for many ecosystem processes (Wardle 2006, Bardgett and van der Putten 2014). When we focussed on these 16 studies, we found that the indirect effects of stressors (how changes in the components of an above- or below-ground community (e.g. taxon or trophic group) can mediate the effects of stressors on the components of another above- or below-ground community) were often discussed (Rantalainen et al. 2006, Hui et al. 2009), but were rarely directly assessed. Instead, these studies mainly focussed on the separate responses of each group. Among the few studies that investigated the indirect effects of stressors, Parfitt et al. (2010) found a strong correlation between the productivity of plant functional groups and the abundance of nematode feeding groups under stress, and Chen et al. (2013) showed that changes in soil microbes and nematodes, and in nutrient resources, mediated the effects of soil acidification and aluminium on plants using structural equation models.

Studying stressors' effects on multiple trophic groups is a first step to reach a better understanding of chemical stressors indirect effects. The next step will be to address how stressors modify food webs and species interactions (Relyea and Hoverman 2006, Clements and Rohr 2009). Here, papers investigating the response of trophic structures to chemical stressors were mainly addressing specific soil fauna groups such as nematodes (Yeates et al. 1994, Dawson et al. 2003,

Sublette et al. 2007, Parfitt et al. 2010, Chen et al. 2013, Naveed et al. 2014), oribatid mites (Parfitt et al. 2010) or other decomposers (Vincent et al. 2018). Future studies could incorporate other above- and below-ground trophic guilds as well (Voigt et al. 2007, Tsiafouli et al. 2015). Ecological network approaches (Hines et al. 2015, Buzhdygan et al. 2020), path analysis and structural equation modelling (Scherber et al. 2010, Eisenhauer et al. 2015, Barnes et al. 2017), as well as multitrophic energy flux calculations (Barnes et al. 2018, Gauzens et al. 2019) should be considered. This would allow to observe the synergistic, antagonistic or additive effects of stressors on different trophic levels and lead to a better understanding of indirect stressor effects on multitrophic biodiversity, ecosystems functions and stability (Clements and Newman 2006, Rohr et al. 2006, de Vries et al. 2013). Disentangling direct and indirect effects of chemical stressors on biodiversity will further allow us to establish a more comprehensive framework regarding the effects of chemical stressors on ecosystem functioning (De Laender et al. 2016). Multitrophic studies and food web approaches will be crucial to reach that end (Hines et al. 2015, Barnes et al. 2017, Seibold et al. 2018, Eisenhauer et al. 2019).

Ecosystem functioning

Changes in biodiversity can have cascading effects on ecosystem functioning (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2012). We found that 43 out of 274 studies addressed the consequences of chemical stressors for at least one ecosystem function (Fig. 3B, Supporting information). It is important to note that this result represents studies that framed their research in terms of ecosystem functioning ('Method' section) and may not represent the full breadth of papers that measured ecosystem processes. Nevertheless, this result points to the lack of knowledge about the functional consequences of chemical stressors and their relation to soil biodiversity changes (Beaumelle et al. 2020).

Most of the 43 studies that we identified addressed ecosystem processes related to nutrient cycling like litter decomposition ($n=18$), primary productivity (plant biomass, productivity, growth or crop yield, $n=16$), respiration ($n=14$) or microbial activity measurements (different enzymes, $n=5$). Fewer studies incorporated measurements of biological pest control ($n=3$) and soil physical properties such as water infiltration, soil compaction or nitrogen leaching ($n=3$). A few studies considered multiple ecosystem functions ($n=16$), but none calculated a multifunctionality index (Byrnes et al. 2014, Manning et al. 2018). These studies often used multiple facets of ecosystem functioning in order to evaluate soil health (Shukurov et al. 2014, Vincent et al. 2018). It would be interesting to improve our knowledge about the impact of chemical stressors on an ecosystem's ability to simultaneously maximize different functions (multifunctionality), especially for functions associated with different types of ecosystem services (Manning et al. 2018, Giling et al. 2019).

Here, the ecosystem functioning studies often related their findings to the concepts of soil health or soil quality without explicitly incorporating the framework of ecosystem services. The functions covered by the studies were mostly related to supporting (nutrient cycling, soil formation and primary production) and provisioning services (food production). However, regulating services (soil detoxification, water purification and waste treatment (MEA 2005)) were far less investigated, despite being particularly relevant in polluted environments. Soil is often the first ecosystem impacted by chemical stressors (e.g. pesticides in agroecosystems, atmospheric deposition of contaminated particles), and can further prevent the transfer of chemicals into aquatic ecosystems or into crops consumed by humans (Cui et al. 2004, Keesstra et al. 2012). Soil components can bind persistent chemical stressors so that they are no longer bioavailable, or no longer released into water bodies. Soil fauna play significant roles in such stabilization processes by their direct impacts on soil characteristics and on plant growth (Sizmur and Richardson 2020). In addition, the accumulation of persistent chemicals in soil organisms (Beaumelle et al. 2017) could have important consequences for the fate of those chemicals in soils and in higher trophic levels (biomagnification), but those processes are still poorly understood (Haimi 2000). Future research is needed to understand how the accumulation of persistent chemicals in soil fauna contributes to the ecosystem services of soil detoxification, water and air purification and pollution attenuation (MEA 2005, Morel et al. 2015). Indeed, organic chemical stressors (such as pesticides and PAHs) can be degraded in soils by specific soil microbes (e.g. for pesticides: Arias-Estévez et al. 2008, for PAHs: Das and Chandran 2011). Among the 43 studies investigating soil ecosystem function responses to chemicals, two studies assessed the potential of soil detoxification by measuring the abundance of soil bacteria able to degrade PAHs (Duncan et al. 2003, Vincent et al. 2018). Laboratory experiments suggest that earthworms improve the microbial degradation of various organic pollutants (Hickman and Reid 2008). The role of soil fauna communities to provide habitats and suitable conditions for microbial degraders involved in soil detoxification deserves further attention. Advancing our understanding of regulating ecosystem services in contaminated soils, and the contribution of soil fauna, is therefore an important future research direction.

A few of the ecosystem functioning studies tested the relationships between biodiversity and ecosystem functions under the influence of chemical stressors (Creamer et al. 2008, Naveed et al. 2014). We found that studies more often correlated ecosystem functions to soil fauna abundance than to soil fauna diversity (Pedersen et al. 1999, Shukurov et al. 2006, Scholz-Starke et al. 2011). Chemical stressors lead to concomitant changes in the abundance and diversity (Hogsden and Harding 2012) thereby complicating the derivation of biodiversity–ecosystem functioning relationship (Beaumelle et al. 2020). However, investigating such biodiversity-mediated effects of stressors on ecosystem functioning,

when biodiversity changes are non-random, is a crucial ecological question (De Laender et al. 2016, Eisenhauer et al. 2019). Furthermore, chemical stressors could alter the magnitude of the biodiversity–ecosystem functioning relationship, with crucial implications for management and future predictions (Baert et al. 2018, Benkwitt et al. 2020).

Overall, we highlight that the consequences of chemical stressors for soil ecosystems and the crucial role of soil fauna communities as mediators of such effects are key research priorities in soil community ecotoxicology. Multifunctionality approaches addressing ecosystem functions related to soil detoxification and nutrient cycling ecosystem services, and their potential synergies (for instance between carbon and pollutant sequestration in soils), would be particularly relevant in the future (Giling et al. 2019).

Interactive effects of multiple drivers of global change

A number of studies investigated the joint impacts of chemical stressors and other global change drivers ($n=82$, Fig. 3C, Supporting information). Most of the 82 studies addressed nutrient enrichment ($n=37$), land-use intensification ($n=28$) and land-use change ($n=22$) in addition to chemical stressors. Our results point to major gaps of knowledge regarding the response of soil communities to the interactions between chemical stressors and climate change ($n=5$ studies), invasive species ($n=1$) and habitat fragmentation and loss (no studies). Indeed, few ($n=24$) of the multiple-driver studies adopted full-factorial design to quantify interactive effects. Multiple-driver studies often compared the individual effects of different drivers (Liu et al. 2012), or only included treatments combining multiple drivers (Pritekel et al. 2006).

We did not expect to find so few studies on the combined effects of chemicals and climate change. Climate change is one of the main drivers of future biodiversity loss (IPBES 2019), and changes in precipitation are expected to have negative effects on soil biodiversity (Blankinship et al. 2011). Moreover, temperature and water availability can modify the sensitivity of organisms to chemical stressors. Warmer climates have been shown to increase the sensitivity of soil organisms to chemicals (Holmstrup et al. 2010). Climate change could further modify soil organisms' exposure by altering their feeding activity, and the rate of degradation of organic chemicals such as pesticides (De Silva et al. 2010). Several studies have also demonstrated that exposure to contaminants decreases soil organisms' tolerance to drought (Sørensen and Holmstrup 2005, Long et al. 2009). Two studies included in the present review found that micro-arthropods and enchytraeids exposed to copper were not more vulnerable to drought than un-exposed communities (Maraldo et al. 2006, Holmstrup et al. 2007). However, Kools et al. (2008) showed that warming had stronger effects on nematode diversity and ecosystem functions in polluted soils. Thus, two important questions remain to be addressed: How will contaminated soil ecosystems respond to additional abiotic stress related

to warmer and drier climates? And how will climate change affect the sensitivity of soil communities to chemicals? Future research could take advantage of existing experiments such as Ecotrons, climate chambers and FACE experiments, in order to conduct full factorial experiments combining realistic climate change scenarios and relevant chemical stressors (De Boeck et al. 2015, Korell et al. 2020).

Our review further reveals that chemical stressors' interactions with biological invasions, and habitat fragmentation remain poorly understood (although it should be noted that habitat fragmentation was the least represented global change in the global meta-analysis) (Phillips et al. 2019a). Only a single study addressed the combined effects of chemicals and invasive species (Pritekel et al. 2006). The management of invasive species often involves the use of synthetic chemicals such as pesticides (Simberloff 2014). Scenarios where soil biodiversity faces both biological invasions and pollution by pesticides are therefore likely to occur, making it an important multiple-driver scenario to consider in future research. Similarly, interest in interactions between chemical stressors and habitat fragmentation or loss is increasing in soil-biodiversity literature, especially in urban ecosystems, where soil habitats are both highly fragmented and subjected to air pollutants such as pharmaceuticals and metals (Ramirez et al. 2014, Caruso et al. 2017, Fenoglio et al. 2020). However, there was no study on the combined effects of chemical stressors and habitat fragmentation or loss in the present review. Future research is necessary to better understand and protect soil biodiversity under these important multiple-driver scenarios.

The multiple-driver scenarios that were most studied were related to agricultural management (land-use intensification (mostly agricultural practices such as tillage) and nutrient enrichment (mostly fertilizer use)). This result echoes the fact that one of the most pressing challenge for humanity is to reduce the negative impacts of agricultural intensification on biodiversity, while providing food for a growing human population (Bommarco et al. 2013, IPBES 2019). Towards that end, a major step forward will be to disentangle the individual and interactive effects of different components of land-use intensification, especially pesticides from other agricultural practices (Geiger et al. 2010). Here, of the 28 studies that investigated the impacts of both chemical stressors and land-use intensification on soil fauna, 9 conducted full factorial experiments enabling to test for their interactive effects (and 9 out of 37 studies for nutrient enrichment). Furthermore, many studies were agronomic studies aiming to improve the profitability of a given crop by combining different specific agricultural practices, while reducing negative effects on soil fauna and soil health (Andersen et al. 2013, Liu et al. 2016). We find that the ability to compare these studies, and to conduct meta-analysis of interaction effects, is currently limited, even for common stressor-intensification combinations such as tillage and pesticides ($n=5$). Therefore, our results call for coordinated efforts that would use fully factorial experiments to test the effects of pesticide use and of the main aspects of

land-use intensification (such as tillage). Such an approach is necessary to design agroecosystem management practices with limited negative impacts on soil biodiversity.

Understanding and predicting the interactive effects of multiple drivers of global change remains a main challenge for ecology (Galic et al. 2018, Rillig et al. 2019, Bowler et al. 2020). We show that this is particularly the case in the field of soil community ecotoxicology, possibly due to the fact that chemical stressors are rarely addressed in global change ecology (Bernhardt et al. 2017, Mazor et al. 2018). Our results point to the specific multiple-driver scenarios that deserve future attention, and will help to prioritize future experimental designs aiming to tackle this crucial question.

Perspectives – future directions

Our literature review highlights that the main knowledge gaps in soil community ecotoxicology research lie at the interface between three important research topics: multitrophic biodiversity, ecosystem functioning and multiple drivers of global change. Within our literature corpus, only three studies addressed those three topics together (Fig. 3D). It is interesting to note that studies investigating ecosystem functioning in parallel to soil fauna responses, often included responses of microbial and plant communities (Fig. 3D). This exemplifies the importance of linking the three above-mentioned research areas. Many ecosystem functions are the results of interactions between soil fauna and microbes, and between above-ground and below-ground organisms (Wardle et al. 2004). Therefore, understanding ecosystem functioning responses to chemical stressors needs to consider multi-trophic biodiversity and biotic interactions (Bruder et al. 2019). In addition, it will not be possible to forecast future soil biodiversity and

ecosystem functioning without accounting for multiple drivers of global change (Rillig et al. 2019), including chemical stressors (Schaeffer et al. 2016). Figure 4 depicts a conceptual framework to implement and test hypotheses regarding multitrophic and multifunctional consequences of global change involving chemical stressors in soil ecosystems.

In order to efficiently incorporate these three research areas, collaborations and global initiatives (experiments and networks) (Schaeffer et al. 2016), as well as long-term monitoring (Yamamuro et al. 2019), will be crucial tools that could be developed on the long run (Table 1). On smaller time scales, targeted experiments in controlled conditions, as well as case studies focussing on neglected taxonomic groups (Fig. 2B) or neglected ecosystem processes, could address critical knowledge gaps (Table 1).

Conclusions

Understanding if and when soil fauna diversity is threatened by chemical stressors will be crucial to forecast future trends in soil biodiversity under current global change scenarios (Geisen et al. 2019b). Our comprehensive review of the literature identifies key recommendations for future research that could guide such efforts. The wide diversity of chemical stressors and the complexity of soil ecosystems calls for global initiatives and collaborations (such as syntheses and global experiments). Such initiatives will enable to explicitly link the responses of multiple taxonomic groups, both above and below the ground, with that of multiple ecosystem functions involved in different facets of ecosystem service provisioning (Manning et al. 2018), and to address the combined impacts of chemical stressors and other aspects of global change such

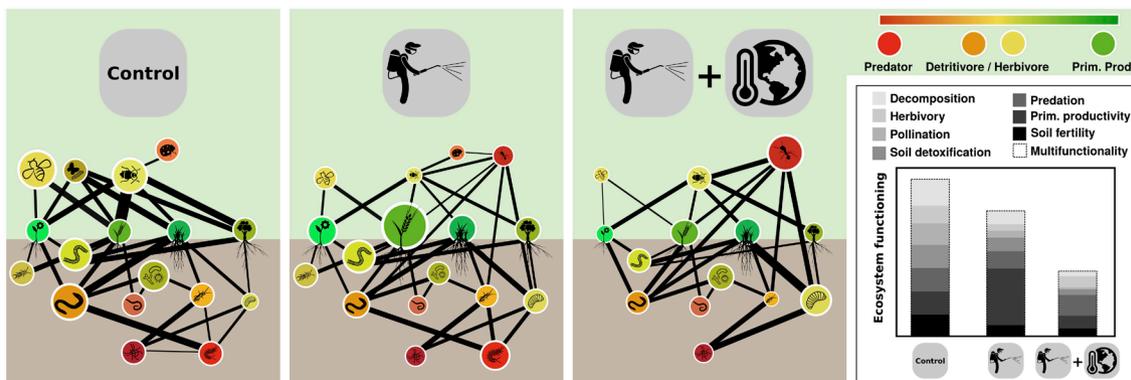


Figure 4. Perspectives for soil community- and ecosystem-ecotoxicology: linking multitrophic diversity and food webs to the functional consequences of chemical stressors and their interactions with additional global change drivers. Drawings depict example hypotheses of how chemical stressors (e.g. pesticide spray, middle panel), and their interaction with climate change (right panel), can alter plant–soil food webs and above- (green background) and below-ground (brown background) interactions compared to control conditions (left panel). Black feeding links with link strength proportional to line width, between different trophic levels, depicted by a color gradient: from primary producers (green shades), over herbivores and decomposers (orange and yellow shades), to predators (red shades). The barplot (right black and white inset) represents potential effects of the different global change driver combinations on multiple ecosystem functions and overall multifunctionality. Sources of symbols: Phylopic, Florian Schneider, and The Noun Project: Gan Khoon Lay, Adrien Coquet, chicabubble, Saeful Muslim, Lluís Pareras, amantaka, Hamish, Alice Noir, Creative Stall, Oliver Kitzler, Pedro Santos, ProSymbols, Richard, Yu luck; partly altered.

Table 1. Future research directions on chemical stressor effects on soil biodiversity. List of research approaches that could be engaged at different time scale to improve understanding and future projections. References indicate seminal works and/or inspiring studies that implemented such approaches on other research topics or other systems.

| | Short term goals | Mid-term goals | Long term goals |
|--|--|---|--|
| Global syntheses | <ul style="list-style-type: none"> – Fill geographical and taxonomic gaps – Syntheses for well-covered groups and chemicals (Phillips et al. 2019a) | <ul style="list-style-type: none"> – Effects of multiple chemical stressors (De Laender 2018, Schäfer and Piggott 2018, Burgess et al. 2020) | <ul style="list-style-type: none"> – Global initiatives and networks across taxonomic groups (Maestre and Eisenhauer 2019) |
| Multi-trophic biodiversity and food webs | <ul style="list-style-type: none"> – Soil multi-diversity approaches (incorporating multiple soil fauna groups across body size categories) (Geisen et al. 2019a) | <ul style="list-style-type: none"> – Soil food web responses (implement network, food-web approaches) (Tylianakis and Morris 2017) | <ul style="list-style-type: none"> – Indirect effects of chemical stressors in light of above-belowground linkages (Wardle et al. 2004, Clements and Rohr 2009) |
| Ecosystem functioning | <ul style="list-style-type: none"> – Functions related to soil detoxification (Ai et al. 2018, Bandowe et al. 2019) – Multifunctionality (Manning et al. 2018, Giling et al. 2019) | <ul style="list-style-type: none"> – Biodiversity–ecosystem function relationships under chemical stressors (mesocosms experiments, Ecotron, ...) (De Laender et al. 2016, Baert et al. 2018) – Role of soil fauna in soil detoxification (Hickman and Reid 2008) | <ul style="list-style-type: none"> – Linking multi-trophic biodiversity and food web responses to ecosystem functioning (Hines et al. 2015, Soliveres et al. 2016, Barnes et al. 2018) – Long-term monitoring (Yamamuro et al. 2019) |
| Multiple drivers | <ul style="list-style-type: none"> – Interactions climate – stressors (Holmstrup et al. 2010, De Boeck et al. 2015) – Identify most probable combinations of chemical stressors and other global change drivers (Bowler et al. 2020) | <ul style="list-style-type: none"> – Food web approaches to better understand the role of species interactions in synergistic and antagonistic effects (Bruder et al. 2019) | <ul style="list-style-type: none"> – Global field experiments with full factorial designs (e.g. Nutrient-Network (Borer et al. 2014), Drought-Network (<https://drought-net.colostate.edu/>), PanDiv experiment (<https://allanecology.com/projects/pandiv/>)) |

as climate change. Such scientific effort is critically needed given that chemical stressors increase at alarming rates, with unknown consequences for natural soil communities.

Code availability

The data (including the full list of references) and R codes necessary to reproduce the analysis and figures presented in this paper can be accessed from github: <<https://github.com/leabeaumelle/ReviewSoilPollution>>.

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Author contributions

Léa Beaumelle: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Supervision (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Lise Thouvenot:** Conceptualization

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